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The Anatomy of Chelyosoma Productum Stimpson.

BY

FRANK WATTS BANCROFT.

WITH ONE PLATE.

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BY FRANK WATTS BANCROFT.

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INTRODUCTION.

PART of the material which formst he basis of this study was derived from the collections of the University of California, and the remainder from a very interesting lot of Puget Sound ascidians which the Young Naturalist's Club of Seattle sent to the University for examination. The specimens were mostly alcoholic, but a few were fixed in picrosulphuric or glacial acetic acid.

The investigation was carried on under the direction of Professor William E. Ritter, for whose constant kindness, not only in connection with my research, but in many other respects as well, I wish to express my most sincere appreciation.

The genus *Chelyosoma* was established by Broderip and Sowerby (1829) to accommodate the single species *C. macleayanum*, which, since then, has attracted considerable attention and has been examined quite frequently, especially by Danish and Scandinavian authors. In consequence of these investigations many anomalous characters

Sept. 16, 1898.

ascribed to it by the earlier writers have vanished, and its close relationship to *Corella* has been ascertained. But there are still several important points in its structure that remain to be elucidated. Kiaer (1893 and 1896) cites all the important literature dealing with the species. *C. productum*, the only other species[1] of the genus, was described by Stimpson (1864) from specimens collected at Puget Sound; and his very incomplete account was supplemented in 1884 by Drasche's (1884) excellent description of a few individuals from the same locality. So far as I know this species has not been described since that time.

RANGE AND EXTERNAL APPEARANCE.

C. productum undoubtedly occurs all along the Pacific coast of the United States and probably also of British Columbia. The center of its range seems to be in the vicinity of Puget Sound, for the specimens from there are quite numerous and surpass in size any that I have met with in California. In the latter state it has been collected from Point Mendocino in the north to San Pedro in the south, but is nowhere abundant. A few specimens were found on the under sides of rocks, some were obtained by dredging in shallow water, and a few from 80 or 90 fathoms.

The color in the younger individuals is whitish, the test being transparent so that the internal organs can be seen through it. In most of the older individuals, however, the surface is conspicuously coated with an opaque yellow or brownish layer which will be considered more in detail later. Some individuals have the base of the test wrinkled and discolored, while the remaining portion is thin and quite clear.

The shape is very characteristic, in spite of considerable variation, dependent largely upon the age of the individual (figs. 1, 2, 2*a*). The most striking external feature is the oval disk which is divided into the movable plates that have given the name to the genus. It is invariably present, and is anteriorly and dorsally situated, making an angle of about 45 degrees with the main axis. Its plane is not, however, perpendicular to the sagittal plane, but slopes a little towards the left. This slope is corellated with a greater development of the muscles on the left side. In life the surface of the disk is usually plane or convex; the concavity seen in the figures is the result of contraction. The youngest individuals collected (disk 7 to 9 mm. long) are much depressed and attached by a broad base which is parallel to the disk; in fact their shape is much like that of *C. macleayanum.* Of the medium sized individuals (disk 9 to 20 mm. long), one with this depressed shape was found, but the majority present what appears to be the distinctive shape of the species (figs. 2, 2*a*). Here the region posterior to the disk is largely developed, raising the shield behind; and a low ridge is noticed passing from the right posterior portion of the disk diagonally around the posterior part of the animal and down to the left hind corner of the broad base. A few of the larger individuals (disk 25 to 30 mm. long) still retain something of this shape; but most of them have assumed an elongated or clavate form with the attachment at the smaller end and the disk placed obliquely on the free extremity (fig. 1). Most of the low ridge is obliterated, but the anterior part persists and is often sharply compressed, thus forming the "carina" mentioned by Stimpson. The largest individual examined measured 65 millimetres in length, 38 in width (dorsoventral), and 25 in thickness; the disk was 40 by 26 millimetres. The dimensions of an average Puget Sound specimen were: length 45, width 26, thickness 21, and disk 32 by 20 millimetres. All the California individuals were much smaller, the largest having a disk 18 millimetres long.

---

[1] Neither Stimpson's (1852) description of *Ascidia geometrica* nor the figure published by Verrill (1874) show that the individuals they examined differ in the least from *C. macleayanum*.

THE DISK.

According to Stimpson and Drasche the disk is divided into fourteen plates, but in the twenty-three individuals I have examined the number is by no means constant. The number of plates, exclusive of those composing the siphons, varied from thirteen to twenty, the different numbers being distributed as follows:

No. of Plates in Disk.	No. of Individuals.
13	2
14	5
15	5
16	2
17	4
18	2
19	2
20	1
15.87	= Average.

But the variation is more than these figures indicate, for, in the groups having the same number of plates in the disk, the arrangement of the plates varied so much that in no case more than three individuals were encountered whose disks were alike in all respects.

There are in all disks three well defined classes of plates:

(1) The *siphonal* plates, which surround the orifices and form the covering of the conical siphon. They are quite constantly six to an orifice. In 24 individuals all had six surrounding the branchial orifice, while one atrial siphon had seven and another five plates. The branchial siphon is almost invariably placed nearer the end of the disk than the atrial, it is usually the longer and the area of its base of attachment is less. Its apex, however, is usually less acute and the plates do not fit so well as in the atrial siphon on account of the greater development of the layer of test on the inside of the siphon.

(2) The *central* plates (*c*, fig. 3), which are placed between the two siphons and are usually two in number. A single one such as occurs in *C. macleayanum* has never been met with; but twice three central plates were encountered, a small median one having been interposed between the other two.

(3) The *peripheral* plates, situated around the edge of the disk. They vary greatly in number, and exhibit bilateral symmetry in about half the individuals examined. In the asymmetrical disks there is a tendency for the number of plates on the right side to be increased. Ten cases of this variation and but three of the opposite one were observed. Figure 3 illustrates a case of this asymmetry. Among the peripheral plates one may distinguish *lateral* ones, the inner ends of which abut, at least partially, against the central plates, and *anterior* and *posterior* ones whose inner ends reach only the siphonal plates. The lateral plates are usually four in number, but occasionally, as in fig. 3, additional ones are found. In some of the lateral plates the corner which is next to the siphon becomes extended (* fig. 3), and occasionally, especially in the broader disks, it is found entirely separated and forming a little accessory quadrilateral plate. The anterior plates are smaller and usually more numerous than the posterior ones. Occasionally the number of peripheral plates is increased by the interposition of small triangular plates which reach neither to the central nor siphonal ones.

Every plate of the larger individuals has its central portion considerably thicker than the periphery (fig. 4), and this change in thickness being quite abrupt is indicated in surface views by a faint line within and parallel to the boundary of the plate. In extreme cases several concentric series of these lines are present. On the other hand, the youngest individuals examined had plates which were of uniform thickness and hence exhibited none of these lines.

UNION OF THE PLATES.

Wagner (1885), who evidently examined the living animals, gives the only correct account of the relations existing between adjacent plates. He says: "Die Ränder der dieses Integument zusammen setzenden Platten erscheinen ziemlich biegsam und weich, wodurch dasselbe an diesen Stellen je nach dem Willen des Thieres ausgedehnt oder verengt werden kann." Sections through this region show that the cause of the flexibility is a local thinning of the test and a more fibrous structure of its matrix (*h*, *h'*, fig. 4). As the change in thickness is always abrupt a very well defined hinge is thus formed. In the contracted condition shown in the figure the hinge appears at the bottom of a groove which is of a narrow V-shape in the younger individuals. In the older ascidians the width increases greatly, so that the cross-section, in the contracted condition, shows the hinge bent nearly double and projecting below the ventral surface of the test. An early stage in this widening of the groove and hinge is shown at *h*, fig. 4. In this condition the approximation of the edges of the groove and the foreign matter that accumulates in it make the boundaries of the plates quite conspicuous. When on the other hand the muscles of the animal relax, the elastic hinges straighten out, the grooves in which they were located become broader and shallower, and the outlines of the plates are consequently much less distinct. The line that bounds the plates peripherally (*p*, fig. 3) has not the same character as the hinges, but merely represents an irregular local thinning and wrinkling of the test.

THE TEST MATRIX.

The consistency of the test is cartilaginous, but, in the disk especially, it is somewhat brittle, cracking when bent much.[1] The matrix is composed of two very distinct layers; an inner, of animal cellulose or tunicin, and an outer one which is not composed of this substance and is much thinner (fig. 4).

The tunicin layer is translucent or transparent. Its matrix is for the most part homogeneous, but fibres are quite plentiful in certain rather variable regions. They always occur quite abundantly in thinnest parts of the test, especially the hinges, and are sporadically encountered in other places. In the disk their direction is parallel to the surface, but in the other parts of the test quite a few prominent fibres are seen running at right angles to the surface.

---

[1] It has been said so often that the test of C. *macleayanum* is horny that one would be tempted to consider the two species quite different in this respect were it not for the description of Swederus (1887) which states that the test is leathery.

The outer layer, which corresponds to the yellow external layer of Löwig and Kölliker (1846), Schulze (1862), and Hertwig (1872), is, as they state, different from cellulose. Towards reagents it behaves like the substance examined by Schulze, giving no blue color with Potassium Iodide and Sulphuric Acid, and being insoluble in concentrated Sulphuric Acid. Boiling with dilute alkali does not dissolve it, but hot concentrated Potassium Hydrate dissolves or at any rate disintegrates the layer. It is slightly harder, stiffer, and more brittle than the tunicin layer, but is formed from it as the sequel will show. In sections it takes a deeper stain than the cellulose, is much more highly refractile, and usually appears homogeneous, but sometimes is differentiated into layers (fig. 5). In some places, however, where it does not seem to be fully formed, it has a more granular appearance. It covers the whole surface of the ascidian, being thinnest on the hinges, a little thicker than the average on the disk, and thickest at the edges of the orifices. It does not cover the surface of the test that extends into the siphons. In addition to covering the surface it is also found within the test in the region of the siphonal ridges which project inwards from the median line of each siphonal plate; but here it occurs in its less compact granular form. As the most powerful muscles of the body are attached to these ridges they must be quite strong; and it seems that the extra supply of yellow substance is introduced to add rigidity to the structure. On the contrary, where flexibility is required, as in the hinge, the thickness of the yellow surface layer is reduced to a minimum and additional fibres added to the tunicin layer.

CELLS IN THE TEST.

All the functionally active cells in the test appear to be of mesodermic origin. In rare cases I have found cells that have been derived from the ectoderm. They have the size and shape of the columnar ectoderm cells, and are found in their best state of preservation in the inner layers of the test, but I have been unable to find a distinct nucleus in any of them. The best occurrence of these cells is shown on the right in fig. 6, and the absence of distinct nuclei is apparent. It must be said, however, that in some places (fig. 10) the nuclei of ectoderm cells that are certainly functionally active have not been differentiated. The distinct nuclei in the proximity of these scattered cells belong to mesodermic cells which may be exercising their phagocytic function. It seems then that ectoderm cells are at times accidentally imbedded in the test, but when there they are no longer able to secrete cellulose and gradually degenerate.

Most of the mesodermic cells are bladder cells. Occasionally, in the innermost layers of the test exceptions are met with in the shape of cells with an abundant granular cytoplasm which entirely fills the cavity of the test they are located in (fig. 7). These, however, are comparatively rare, and as they pass into the outer layers of the test become vacuolated and transformed into typical bladder cells. The latter (figs. 6, 7, 8, 9) are much smaller than the bladder cells in those species of *Ascidia* where they are so greatly developed, and occupy a much smaller proportion of the test. They always present a deeply stained nucleus, but sometimes the cytoplasm and the test cavity which contains it are difficult to make out. The size of the nuclei is quite variable, ranging from that of the ectoderm nuclei to minute, deeply staining bodies one-half or one-third of a micron in diameter. These smaller nuclei seem on the whole to be more frequent in the outer layers. When prepared with most stains the cytoplasm does not seem to extend beyond the wall of the bladder; but a very deep stain, or better still, treatment with Potassium Iodide and Sulphuric Acid brings out quite a number of straight, slender, cytoplasmic processes extending into the test matrix (fig. 8). The size of the cells is much smaller in the densely fibrous parts of the test, and their shape is fusiform instead of oval as in the other parts. If, however, the matrix is homogeneous, the bladder cells nearest to the ectoderm are just as large as those in the center and differ from them only in having in some cases a slightly larger amount of cytoplasm. We see then that as these cells come to lie in the outer layers of the test the cytoplasmic and nuclear material diminishes and the test cavity remains the same.

ORIGIN OF THE YELLOW LAYER.

It has been said that the outer yellow layer of the test is formed by the activity of the cells in the tunicin layer. The steps in the process can be followed quite easily, but unfortunately the principal criterion that must be used in following out the stages cannot be well represented in the drawings. This is the characteristic appearance of the yellow substance due to its homogeneous structure and high index of refraction. In some regions, especially in the siphonal ridges, it is found in a granular, more lightly colored form, thus losing some of its characteristic appearance; but it retains its high refractility and grades insensibly into the more compact form so that there can be no doubt of its identity. The first step in the formation of the yellow substance is the deposition of a thin layer of it in the vicinity of the wall of a bladder cell. The deposit may be of the compact or granular form, and either just within or without the wall of the bladder. Figure 9, *a*, shows a cell with a thin layer of the substance just inside the bladder, *e*, a cell with the substance deposited on the outside only. Figure 9, *b*, represents a stage in which the deposit has been principally within, as shown by the angular vesicle. The size of the deposit about many of the cells, such as *c*, fig. 9, and *a*, *b* and *c*, fig. 5, shows that most of it has been laid down on the outside of the bladder. Appearances like *a* and *b*, fig. 5, where isolated masses surrounding individual cells fuse with the outer layer, are very numerous and the fusion is always perfect, no line of contact being visible at all. This together with the identical appearance of the substance surrounding the cell and that composing the yellow layer shows conclusively the way in which the latter is formed. It does not, however, grow exclusively by incorporating masses that were originally separate, for some cells do not take on this function until they are closely pressed against the outer layer, so that from the first the product of their activity is in contact with this layer. In some cases, especially in the siphonal ridges, a number of cells do not seem to begin forming the yellow substance until they have been nearly or quite surrounded by it. The ultimate fate of the cells in the yellow layer seems to be degeneration, for of those nearest the surface nothing can be seen but a small vesicle containing some refractile material in which usually not even the remains of a nucleus can be made out. As there are extensive regions of the test which contain no blood-vessels at all, the bladder cells must be in great measure physiologically isolated from the rest of the body, for they could receive nutritive fluids only by way of the rather dense cellulose substance. On this account I think it likely that the yellow substance is formed almost entirely by a direct transformation of the cellulose, and accordingly it would be interesting to know the exact chemical relations between the two substances.

BLOOD-VESSELS IN THE TEST.

These are usually confined to the posterior region near the base of attachment, at times extending half way up the free wall towards the disk; but they have never been found extending into the disk. The proximal part of the system is composed of a large number of pairs of vessels running side by side, as in *Ascidia* and other tunicates, but the terminal part in which these two vessels communicate with each other is very greatly developed. It is much more capacious and consists of large single or compound and irregularly branching ampullæ, present in such numbers that the substance of the test is fairly honeycombed in places. Nor are these ampullæ confined to the terminations of the blood-vessels, for one or even several pairs of blood-vessels may enter the cavity from a proximal direction and another pair leave it distally to unite again in some terminal ampulla.

UNION OF MUSCLES AND TEST.

Both Eschricht (1842) and Drasche describe the intimate connection between the muscles and the test, especially in the region of the siphonal ridges; but so far as I know no one has described the means by which this union is accomplished. Wherever a bundle of muscle fibres is attached to the test the latter is produced into a conical or ridge-like papilla to the summit of which the muscles are joined. This attachment is accomplished principally through the intermediation of the ectoderm. The cells of this layer usually form a cubical or thin pavement epithelium which may become vacuolated and very irregular in places, but on the test papillæ the epithelium is always of the columnar form (figs. 6 and 11) and is more actively engaged in secreting cellulose. The increased activity in this region is proved by the presence of the test papilla which can hardly be explained except as the result of this activity, by the larger number and size of the ectoderm cells, and by the pronounced character of the processes that extend from them into the test. These processes have been found by Seeliger (1893, p. 494), Ritter (1893, p. 55), and others, who think that they are in some way connected with the active secretion of cellulose. In addition to subserving this function they insure a firmer union between the test and the ectoderm, but these two layers are nevertheless separated by the strong contractions of the animal. In fig. 10, *a* and *d*, this separation and the processes that have been torn out of the test are shown. In the adjacent sections of this series they are considerably more numerous, and the columnar cells more closely packed together. On the summits of the test papillæ the ectoderm instead of simply covering the papillæ forms convolutions and deep pockets (*pt*, fig. 11) which greatly increase the surface of contact and secretion. The muscle fibres seem to be attached to the ectoderm by means of the connective tissue lining this layer, and can be seen extending down into the ectodermal pockets. The whole contrivance renders the attachment of the muscles so firm that I have not seen a single case where they have been pulled away from the test.

It is probable that another result of these involutions is an occasional cutting off of the end of a pocket by a more rapid secretion near the mouth. The cells which were contained in the deeper portion would then become imbedded in the test matrix and give rise to the occasional ectoderm cells there that have already been described.

THE MUSCULATURE.

The fact that the distribution of the muscles in our species and *C. macleayanum* differs in one important respect has been clearly pointed out by Drasche. He divided the muscles of *C. productum* into four classes: (1) The peripheral muscles, situated around the edge of the disk and extending well towards the center (fig. 11). (2 and 3) The circular and longitudinal muscles of the siphons. (4) The twelve series of more or less fan-shaped muscles radiating from the siphons and attached to the outer ends of the siphonal ridges. In *C. macleayanum*, on the other hand, the peripheral system is much less developed and another system is added which is entirely lacking in all the individuals of the western species that I have examined. This is a system of short muscles joining adjacent plates in the extra-siphonal part of the disk. It appears to be the most fundamental type, for all the other classes are referable to it without difficulty. They all connect the plates with the test on the other side of a hinge-like thinner area, except some of the peripheral muscles of *C. productum*, which extend clear across the peripheral plates and are united to the central ones.

In our species every muscle, except those connected with the siphons, is attached at some place on the disk, extends nearly to the edge of the disk and then bends ventrally and is attached to the side wall of the test some distance down. The inner fibres (the conspicuous ones in fig. 11) are the longest, being attached farthest from the edge of the disk and down the sides of the animal. Besides the inner fibres there are a lot of shorter ones (*m. s*, fig. 11) that are attached nearer the edge of the disk at both ends. The musculature is much better developed on the left side, the fibres being longer and extending much farther down the side. There is a tendency for all of these muscles to be inserted near the centers of the plates, which are indicated by the heavy black lines in the figure. But the variation is so great that this tendency is hardly manifested at all in some regions. It is to be noted, however, that no muscles are ever inserted on the hinges.

In the siphons the radial muscles are weaker and situated internally to the circular ones. Centrally they are attached near the lip of the orifice, and thence extend beyond the region of the siphon, either losing themselves among the peripheral muscles or joining these directly. The circular ones consist of six series of strong fibres extending from one siphonal ridge to the next. A fair average condition of the fan-shaped muscles is seen in the figure. They join the outer ends of the siphonal ridges with the extra siphonal plates, and assist in closing the orifices both directly by their contraction, and indirectly by giving a more rigid support to the contracting circular muscles.

When we compare the two species of our genus, it is found that the arrangement and variability of the plates depend in great measure upon their relations with the muscles. In *C. macleayanum* the plates appear to be very constant in number and arrangement; for among the thirty-four or more individuals of which accounts have been published the only indication of variation is in Swederus' description, where the number of plates is stated to be nine, instead of eight. Five figures of the disk have been printed and in all the plates are the same. Besides these there is one figure of Wagner's which would seem to indicate that the two anterior plates are wanting in that individual; the appearance, however, may be merely due to the perspective. The reason for this constancy lies in the fact that the muscles extend across all the hinges and are perpendicular to them. This is the most stable condition, and deviations of either muscles or hinge would cause no rearrangement, but would tend to be gradually obliterated by the interaction of the two. In accordance with this view we find that in *C. productum*, which is on the whole very variable, the siphons, in which the principal muscles cross the hinges at right angles, are remarkably constant. But on the other hand, the peripheral muscles are nearly parallel to the hinges of that region, and here we have the greatest variability. The conditions are unstable, for a slight deviation in the disposition of the muscles can easily cause a rearrangement. Thus, if in the large lateral plate *l*, fig. 3, a slight massing of the muscles at the two ends might have resulted in the formation of two plates there, just as has occurred on the opposite side. Similarly, the presence of one or more longitudinal hinges between the central plates, which is the most constant difference in the two disks, follows as a mechanical necessity from the arrangement of the muscles. Thus it becomes evident that all the differences in the disks of the two forms are correlated with the great development of the peripheral muscles in *C. productum*.

THE PHARYNGEAL APPARATUS.

The simple filiform tentacles are subject to considerable variation, which is independent of the size of the individual as the following measurements show:

Dimensions of Disk.	Number of Tentacles.
6 x 4	118
10.5 x 6	174
13 x 11.5	480
23 x 18	142
27 x 22	214
30 x 22	123

They are arranged in from two to four concentric rows, the largest ones being situated on the outer side, and the tentacles in adjacent rows alternating with each other in position. The tentacles are often considerably smaller and the rows fewer on the sides of the circle than anteriorly and posteriorly.

There is but one peripharyngeal band present, and since this connects with the edges of the endostyle and the epibranchial groove, it evidently corresponds to the outer of the two bands usually encountered. It is ciliated over its whole surface, and in some preparations appears to fuse with the lips of the dorsal tubercle. However, sections and the best dissections show that it extends posteriorly to the orifice of the tubercle to join the edge of the epibranchial groove.

Little remains to be added to Drasche's account of the relations of dorsal tubercle, hypophysial gland, epibranchial groove, and ganglion. His excellent figure of these organs represents a good average condition of my specimens, except that the ganglion usually has five nerves extending from it posteriorly, and that the hypophysial duct in all of the individuals I examined extends along the left edge of the gland, so that the tubules enter it from the right side only. The shape and positions of these organs is remarkably constant. They are all placed a little to the right of the median line joining the two orifices, exactly as in *C. macleayanum* [1], and their relations to each other were always found to be exactly as in Drasche's figure.

---

[1] Drasche, who states that in this species the dorsal lamina is on the left of the median line, evidently does not understand Eschricht's figures.

The hypophysis is a compound tubular gland with eight or nine tubules emptying into the duct. On account of the thinness of the mantle in this region they are all in the same plane. Anteriorly a corner of the gland is ventral to the ganglion, but posteriorly it is at the same level or dorsal to the latter.

The ganglion usually has a pair of anterior nerves, a latero-anterior pair, and five irregularly arranged ones extending from its posterior end. Variations are, however, quite frequent.

THE BRANCHIAL SAC.

The branchial sac is attached to the mantle along the extent of the peripharyngeal band, epibranchial groove, endostyle, and postbranchial groove, and to the intestine along the whole of its terminal part, which is dorsal to the branchial sac. Many connectives extend to both mantle and viscera, but they have no very definite arrangement on account of the irregularity of the vessels.

The arrangement of the vessels is subject to considerable variation, a large part of which, however, depends upon the age of the individual. Figure 12 shows a portion of the branchial sac of the smallest individual collected. The conditions here are very regular and simple when compared with the older ones; but even in these a careful study shows essentially the same structure. There are four kinds of vessels: (1) The outer vessels (*o*, fig. 12), which occupy the outer surface of the sac and unite with all the connectives. They extend in longitudinal, transverse, and intermediate directions, and bound the spaces in which the spiral stigmata are contained. They are quite conspicuous, especially when seen from without, and contain most of the blood. (2) The spiral interstigmatic vessels, which, together with the outer ones surrounding them, limit the stigmata. In the younger individuals these are in a plane but slightly interior to the outer vessels, but later an increase in surface is effected by drawing the spirals out into cones with their apices extending inwardly. At the same time the stigmata are often turned edgewise, so that in surface views their presence can hardly be detected. In these older individuals the edges of the outer vessels also grow beyond the edges of the stigmata, so that from the outside the latter cannot be seen, but only an irregular lot of spaces leading into the bases of the cones. In the figure it is seen that each spiral is composed of but one stigma, and that often the same stigma may be coiled at both ends and form two spirals. In the more mature condition there are two and occasionally three stigmata to a spiral, but never more nor less, so far as has been observed. (3) The intermediate vessels (*i*, fig. 12). They are very irregular, thin walled, and connect all the other vessels with each other in the most diverse ways. Receiving the blood that has reached the apex of the cone they distribute it to other vessels. One of their most important functions is to bear the connecting ducts which support the internal longitudinal bars. These ducts are often near the place of union of the intermediate vessels with the outer ones (*u*, fig. 12). Among the older individuals these vessels are much more strongly developed and sometimes almost completely mask the spiral vessels and stigmata. They form the most regular transverse vessels that the species possesses, usually, but not always, directly uniting adjacent connecting ducts. This regularity is most pronounced near the endostyle and dorsal lamina. (4) The internal longitudinal bars, which are never papillated. They are fairly regular over the whole surface of the branchial sac except where it is growing most rapidly, along the endostyle and dorsal lamina. In these regions all the stages in their formation from the smallest papillæ to larger ones whose anterior and posterior processes have just united can be seen. The connecting ducts invariably curve so that their inner ends point dorsally, and in the larger ascidians they are often so crowded as to be two or three times as numerous as those in the figure.

As a result of all these processes, the branchial sac in the older individuals is so complex and the regions so different, even in the same animal, that if there were no earlier stages to refer to it would be exceedingly difficult to arrive at sound conclusions concerning the typical relations of the various vessels.

The endostyle, in the preserved specimens, is near the extreme left edge of the branchial sac; but it is probable that in life it was somewhat closer to the sagittal plane, since the more powerful muscles of the left side would draw it away from its natural position. Its posterior end is continuous with the postbranchial groove, the most prominent edge of which connects with the right edge of the endostyle.

The dorsal lamina is represented by a series of languettes which vary from eleven to thirty-two in number. As a rule they are more numerous in the larger individuals. They extend from the posterior end of the epibranchial groove to the edge of the smooth area surrounding the œsophageal orifice, and their concave side is turned towards the right. The great dorsal blood-vessel usually accompanying the lamina runs in the mesentery of the intestine as far as the anus, and thence extends forwards, branching very irregularly. Two strong bands of smooth muscle fibres are contained in the lateral walls of this vessel.

THE VISCERA.

In discussing the position of the viscera, the sagittal plane is best taken as passing through the two siphons and dividing the animal as nearly as possible into symmetrical halves. This will divide the disk into approximately equal parts, except in the few cases where the siphons are considerably nearer the right side, as in Traustedt's (1887) fig. 2. In such cases, however, the plane as defined will be more nearly the plane of symmetry of the whole animal than if it were taken as cutting the disk midway between the two sides and not including the siphons.

This is apparently the plane adopted by Drasche (1884), Herdman (1891), and Traustedt (1880). But the last author in a later paper (1882) defined the sagittal plane as passing through the endostyle and ganglion. As in *C. macleayanum* the endostyle is near the extreme left, and the ganglion on the right of the line joining the siphons; this plane is nearly parallel to the disk, the siphons are on the left, and the viscera on the right side. Though on some grounds this criterion might be justified for *C. macleayanum*, it will hardly serve for the more elongated *C. productum*, in which this sagittal plane would neither contain the long axis of the animal nor divide it into approximately equal parts.

Both Drasche for *C. productum* and Herdman for the whole genus disagree with Traustedt in describing the viscera as located on the left side of the animal, and Kiaer (1893) makes the strange statement that both disk and digestive tract are on the left side. The evidence for some of these statements is seen in the figures of Eschricht (1842), Traustedt (1887), and Wagner (1885). These show that in *C. macleayanum* the viscera are either strictly ventral in position or slightly on the *left* of the median line. In *C. productum*, on the other hand, the specimens that I have examined fail to confirm Drasche's statement, for in them the major part of the digestive tract is on the *right* side of the sagittal plane (fig. 13), and this condition is more pronounced in the more elongated individuals. In the flattest of my specimens, however, the conditions found in *C. macleaynum* are more closely approximated. But more important than the question of determining whether two-fifths or three-fifths of the viscera are on the right of the midventral line is the fact that in both species all of the digestive tract, except the dorsal terminal part of the intestine, is *ventrally* situated.

Although *Chelyosoma*, since its viscera are sometimes on one and sometimes on the other side of the median plane, shows how the change from the *Corella* to the *Ascidia* condition might be effected without passing through a stage like *Ciona*, I do not believe that it represents such a transitional condition, for the curve of the intestine is exactly like that of *Corella*. Furthermore, the position of the heart, which in *C. productum* is on the side of the stomach farthest from the midventral line, still more increases this similarity. As the general course of the digestive tract in our species is exactly like that of *C. macleayanum* a detailed description is unnecessary.

The epithelium of the ventral wall of the stomach is thrown into folds forming a deep groove which extends from the entrance of the œsophagus to the exit of the intestine. From the outside these appear as a series of longitudinal lines that have often been described. The rest of the stomach has its surface area increased by the formation of pocket-like projections which give it a very characteristic appearance in the surface view (fig. 14). A reticulate gland with a single duct opening into the stomach covers its pyloric portion and the adjacent intestine. This gland presents all the features of the one described by Winiwarter (1895), except the large number of separate ducts. The intestine is quite simple and does not possess a typhlosole.

The sexual organs are much like those described for *C. macleayanum* by Wagner. Both ovary and testis are a complicated system of dichotomously branching tubes which never reunite. They extend both ventrally and dorsally to the digestive tract, and in the older individuals, with the assistance of the pyloric gland, they completely cover it. Their ducts follow the course of the intestine and open in the immediate vicinity of the anus. Figure 14 represents these organs in a young animal.

CONCLUSION.

This account of the structure of *Chelyosoma* shows that it is even more closely related to *Corella* than was formerly supposed. In fact, it agrees with *Corella* in all the characters which differentiate the latter from *Ascidia*. On the other hand, all of its distinguishing characteristics are of a very exceptional kind. Thus, the division of the test into plates is shared by only one other species of tunicate, *Forbessella tessellata*, while the attachment of the muscles and their definite relations with the plates are, so far as known, unique. The lacunar character of the blood-vessels in the test, asymmetrical hypophysial gland, and single peripharyngeal band are also unusual.

Of the two species of the genus, *C. macleayanum* presents on the whole fewer aberrant characters and is nearer the direct line of descent from some Corella-like ancestor. Its exceedingly depressed form is more unusual than the shape of the western species; but on the other hand, the youngest individuals of *C. productum* are very much flatter than the older ones, thus indicating a depressed ancestor. The difference in the musculature also furnishes very strong evidence for believing *C. macleayanum* the more primitive type; for we can easily see how a division of the test into plates with the muscles extending perpendicularly to the hinges might be developed from a form with an irregular mass of muscles confined to the dorsal side of the animal. Then, when the plates are once formed, the condition in *C. productum* could be obtained by increasing the peripheral muscles. On the other hand, it is very difficult to see how the peripheral plates could ever have been developed directly by a system of muscles extending parallel to the hinges. In the more recent development of *C. productum* then, we have what appears to be the reason for its unstable condition, and the attendant variability in those characters which distinguish it from the other member of the genus.

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EXPLANATION OF PLATE XVIII.

All the figures except Nos. 1, 2, 2*a*, and 13 were drawn with the aid of the camera.

Fig. 1. A large Puget Sound individual from the left. Natural size.

Fig. 2. A regularly shaped California individual from the left; x2.

Fig. 2*a*. Same individual; dorsal view.

Fig. 3. The disk, showing the arrangement of the plates, and the lines indicating the boundary of their central thickened portion; *br*, branchial siphon; *at*, atrial siphon; *c*, central plates; *l*, lateral plates; *p*, peripheral folds; * points where the accessory central plates may be formed. Natural size.

Fig. 4. Cross-section through a plate and the two hinges *(h, h')* at its edges, showing the yellow layer *(y. l)*, test papillæ *(t. p)*, and ectoderm *(ec)*; x28.

Fig. 5. The yellow layer, more highly magnified, showing an isolated mass of yellow substance surrounding a bladder cell *(c)* and two masses *(a, b)* which have just fused with the yellow layer; x 830.

Fig. 6. Section through the ectoderm and part of the cellulose layer, showing the remains of ectoderm cells imbedded in the latter; x 830.

Fig. 7. A group of bladder cells.

Fig. 8. Bladder cells, overstained in Iron-Hæmatoxylin to show their slender processes into the test; x 830.

Fig. 9. Various stages in the formation of the yellow substance about the bladder cells; x 830.

Fig. 10. A test papilla showing the attachment of a muscle fibre *(m)* by means of the ectodermic pockets *(pt)*; *a* and *d* are the points where the ectoderm has been torn from the test; x 380.

Fig. 11. The muscles of the disk from within; *m. s*, the short exterior muscle fibres; *pc. b*, the peripharyngeal band. The outlines of the plates are indicated by the heavy black lines; x 2.

Fig. 12. Branchial sac of a very young individual; *o*, outer vessels; *i*, intermediate vessels; *u*, points of union between the outer and intermediate vessels; x 130.

Fig. 13. An individual with the ventral part of the test removed, from the right side, showing the course of the digestive tract. *indicates the position of the heart; x 2.

Fig. 14. A younger individual; ventral view, but slightly from the right, showing the ovary *(o)* and testis *(t)*. Test entirely removed; x 5.

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